PIPESTELA, A NEW GENUS OF AXINELLIDAE (PORIFERA: DEMOSPONGIAE: HALICHONDRIDA) AND DESCRIPTION OF THREE NEW SPECIES

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The new genus *Pipestela* is created to include axinellid sponges with lamellate, branching or tubular growth form bearing mainly oxeas arranged in a distinctive loose skeleton of vaguely plumose and wavy spiculo-fibres. The genus is known only from northeastern Australia, from the Great Barrier Reef, Coral Sea, Papua New Guinea, Solomon Islands and Vanuatu, with a single specimen known so far from Western Australia. Type species *Pipestela candelabra* sp. nov. is the most widely distributed of the five known species, and in some places forms highly abundant local populations. *Pipestela rara* sp. nov., *P. occidentalis* sp. nov., *P. hooperi* (Van Soest et al.) n. comb. and *P. terpenensis* (Fromont) n. comb. are also assigned to this new genus. All species are associated with coral reefs, in relatively clear water, between 10–50m depth. The genus shows affinity to *Cymbastela* in the predominance of oxeas, and to *Auletta* by the common organ-pipe morphology, but is distinct from the former by the loose skeleton and from the latter by its lack of styles and wavy diactinal spicules. The phylogenetic relationships of *Pipestela*, its position in the higher classification, and the limits of its spatial distribution are further investigated. The definition of *Cymbastela* is revised as a consequence of erecting this new genus ☐ *Porifera, Demospongiae, Axinellidae, Pipestela n. gen., new species, coral reef sponges, Cymbastela, revision.*

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According to the revision of Alvarez & Hooper (2002) the family Axinellidae now includes ten genera: *Auletta, Axinella, Cymbastela, Dragmacidon, Dragmaxia, Pararhaphoxya, Phakellia, Phycopsis, Ptilocaulis* and *Reniochalina*. Both the family and its genera lack synapomorphies, instead diagnosed by unique combinations of plesiomorphic characters that ultimately create ambiguities for the allocation of species – particularly those with intermediate or modified characters. Other types of evidence, such as molecular DNA sequences or bio-organic chemistry (Alvarez et al., 2000; Erpenbeck et al., 2005), indicate that Axinellidae and some of its genera (e.g. *Axinella*) are polyphyletic taxa. Therefore, despite the types of characters, or the combination in which they are used within the current systematics, only few genera of this family can be distinguished currently beyond reasonable doubt. This present paper is a contribution to resolve these inconsistencies within the current systematics.

Sponges of the family Axinellidae are currently allocated to the order Halichondrida (Alvarez & Hooper, 2002), and defined by the absence of a specialised ectosomal skeleton, the characteristics of the surface, the architecture of the choanosomal skeleton and spicule geometries. Axinellidae exhibit a great diversity of shapes (e.g. encrusting, massive, branching, fan-shape, lamellate, tubular), although erect or stalked, arborescent branching forms are common. Colour is frequently within or close to the red spectrum being commonly shades of carotenoid pigments, including red, orange, yellow and brown. The choanosomal skeleton is often compressed in the axis, creating a differentiation between axial and extra-axial regions, particularly evident in species with branching and arborescent shapes. Compression of the skeleton is also observed in the peduncle of stalked species. Plumose spicule-fibres or tracts of oxeas, styles, or both, are generally a common feature among axinellid species. The presence of oxeas and styles in the same size category is also a distinctive feature of most axinellid sponges but in some species one

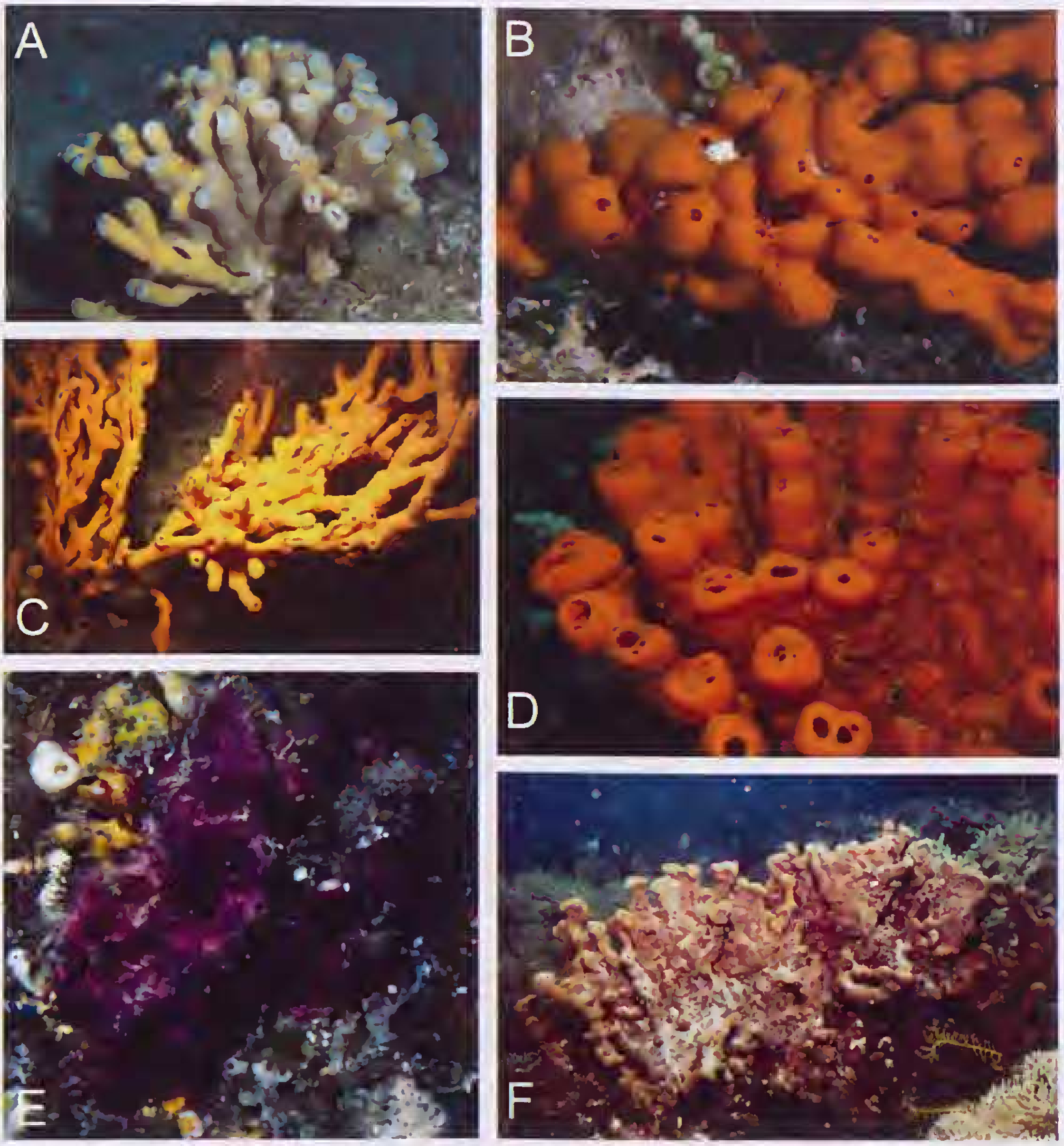

FIG. 1. A–D, Different growth forms of *Pipestela candelabra* sp. nov. *in situ*. A, 0CDN1949-C. B, 0CDN1807-X (paratype). C, QMG312951. D, 0CDN8208-H. E, *P. rara* sp. nov., QMG 319301, holotype photographed *in situ*. F, *P. terpenensis* comb. nov. *in situ*, NTMZ004057.

or the other spicule type may be absent or rare (e.g. *Cymbastela* spp. having only oxeas, or *Ptilocaulis* spp. having mainly styles).

The family Axinellidae has a cosmopolitan distribution and according to the World Porifera Database (http://www.vliz.be/porifera/index.php) currently includes 342 valid species. Previous revisions at regional levels record 15 species for New Caledonia, 11 for New Zealand, 21 for the Central-West Atlantic region, and 17 for the NE Atlantic (Alvarez & Hooper, 2002 and references within). At least 57 axinellid species are represented in Australia (Hooper & Wiedenmayer, 1994, with subsequent updates available online, 2004) but no regional revision of the fauna has so far been undertaken, and this estimate requires closer confirmation. Studies in progress, and limited at this stage to northern Australia (Alvarez and Hooper, unpublished data), indicate that at least 60 species of Axinellidae are represented across the northern region of Australia. One of these species is a very common sponge found throughout the Great Barrier Reef, Coral Sea in Australia, Papua New Guinea and adjacent regions, and is here assigned to a new genus and species with features that agree with the definition of Axinellidae, and in particular with some apparent affinities to the genera *Auletta* and *Cymbastela*. The genus is erected to accommodate this species and several less common sponges bearing mainly oxeas as in *Cymbastela*, but lacking its characteristic cup-shape, and with distinctive loose skeletons of vaguely plumose and wavy spicule-fibres dissimilar to the highly spiculose and tightly meshed spicule tracts found in *Cymbastela*.

METHODS

Sponge collections acquired by the authors and others throughout northern Australia and the Indo-Pacific were examined in the institutions listed below. Specimens were prepared for light microscopy using the usual methods (e.g. Van Soest & Hooper, 2005). Spicule measurements are based on 25 spicules of each category and denoted as range (and mean ± 1. S.E.) of length and width. Measurements were made using a digital video camera attached to a light microscope in combination with the software V++ Precision Digital Imaging System v 4.0 (© Digital Optics, Ltd). The higher systematic arrangement follows Hooper & Van Soest (2002).

ABBREVIATIONS. CRRF, Coral Reef Research Foundation, Palau. GBR, Great Barrier Reef. MHNG, Muséum d'Histoirie Naturelle, Geneva. MSNG, Museum of Natural History of Genoa. NCI, U.S National Cancer Institute collections. NTM, Museum and Art Gallery of the Northern Territory (formerly Northern Territory Museum), Darwin. ORSTOM (now IRD), Institut de Recherché pour le Développement (IRD Noumea), New Caledonia. QM, Queensland Museum, Brisbane. ZMA, Zoologisch Museum, University of Amsterdam, WAM, Western Australian Museum.

SYSTEMATICS

Class DEMOSPONGIAE Sollas, 1885
Order HALICHONDRIDA Gray, 1867
Family AXINELLIDAE Carter, 1875

Pipestela gen. nov

DEFINITION. Axinellidae with choanosomal skeleton formed by a loose reticulation of plumose and wavy paucispicular to multispicular tracts of relatively thin oxeas.

DIAGNOSIS. Lamellate, branching or tubular growth form. Surface smooth, consistency elastic, rubbery. Ectosomal skeleton not specialised. Choanosomal skeleton slightly compressed toward the axis or centre of sponge, formed by a loose reticulation of plumose and wavy multispicular to paucispicular tracts coring ill-defined spongin fibres in some cases. Primary spicule-fibres connected by secondary thinner and shorter tracts, uni- or paucispicular. Interstitial free spicules abundant. Megascleres are thin oxeas, curved, flexuous or sinuous, often with asymmetrical ends and a wide axial channel frequently visible. Some with stylote modified ends.

TYPE SPECIES. *Pipestela candelabra* sp. nov. (here designated)

ETYMOLOGY. English for pipe and Latin *–stela-* for column; *Pipestela*, reflecting the predominant growth form of the type species. Gender: feminine.

DISTRIBUTION. Common on the Great Barrier Reef, Papua New Guinea and Solomon Islands, with outlying populations in the Coral Sea territories, northwestern Australia and Vanuatu.

REMARKS. The genus is erected to include the type species, two less common species *Pipestela rara* sp. nov. *P. occidentalis* sp. nov., and two other species previously assigned to *Cymbastela*, *P. hooperi* (Van Soest et al., 1996) and *P. terpenensis* (Fromont, 1993). These species share most skeletal features with slight variation in the size and general shape of oxeas. The wavy thin spicule tracts of oxeas encased in ill-defined spongin fibres are reminiscent of some haplosclerid genera, such as *Amphimedon* Duchassaing de Fonbressin & Michelotti, 1864 which was the original allocation of *P. terpenensis*. However, *Amphimedon* has a specialised ectosomal skeleton that is absent in *P. terpenensis*. Further, recognised species of *Amphimedon* across the Indo-Pacific, are typically blue spectrum colour (blue, grey, lilac, green, tan). With the exception of *P. hooperi* all species develop tubular or cylindrical projections with oscula either at the apex of tubes or on the lateral sides of the tubes/branches. Within Axinellidae, this type of growth form is seen in *Auletta* Schmidt, 1870, but that genus has a clearly reticulated skeleton of robust styles and sinuous strongyles.

Pipestela candelabra sp. nov

(Figs 1A–D, 2, 3)

Clathria sp.; Mead & Beckett Publishing, 1984: 159 (top figure)

Auletta sp.; Colin & Arneson, 1997: 31, 36, 37, 121, figs 59, 89, 90, 121

Axinella sp.; Colin & Arneson, 1997: 37, fig. 92

Auletta constricta; Crews et al., 1994: 2932; Hooper et al., 1999 : 259; Sonnenschein et al., 2004: 779.

Not *Auletta constricta* Pulitzer-Finali, 1982: 95, fig. 6.

Pseudaxinyssa sp.; Silva, Andersen & Allen, 1990: 489.

Cymbastela sp.: Coleman, Van Soest & Andersen, 1999: 1137.

MATERIAL EXAMINED. HOLOTYPE: QMG320790, Houghton Reef, Howick Grp, GBR (northern sector), 14°31.1901' S,144°58.9' E, 20 m, 3.07.2003.

PARATYPES: QMG320362, JEWELL REEF, N OF CAPE FLATTERY, GBR (NORTHERN SECTOR), 14°25.99' S,145°21.42' E, 15m , 28.06.2003. QMG303078, NE Cape Grenville, Shelburne Bay CSIRO stn.26, GBR, 11°30.1001' S,143°4.04' E,

TABLE 1. Comparison of spicule dimensions among species of *Pipestela*. Measurements in micrometres.

Specimen	Locality	Length	Width
Pipestela candelabra			
	GBR, Northern sector		
QMG320790 (holotype)	Houghton Reef	158.29–234.9 µm (195.88±20.52)	2.44–5.05 µm (3.76±0.71)
QMG320362 (paratype)	Jewell Reef	131.34–213.94 µm (173.32±22.22)	1.87–5.62 µm (3.91±0.91)
QMG303078 (paratype)	NE Cape Grenville	117.47–205.06 (164.52±24.95)	1.06–3.67 (2.42±0.51)
	Papua New Guinea		
CRRF 0CDN1801-X (paratype)	Coral sea SW Port Morsby	153.57–219.35 µm (191.97±19.58)	1.99–3.37 µm (2.73±0.5)
QMG312951	Keppel Pt	191.9–547.24 µm (352.09±114.56)	3.45–10.79 µm (6.14±1.69)
0CDN8208H	Woodlark Is	145.49–217.8 (173.06±17.87)	2.27–3.98 (2.76±0.47)
	GBR, Cairns–Cooktown sector		
QMG304178	Lizard I.	124.7–208.43 (184.2±19.53)	1.71–4.59 (3.25±0.7)
QMG307657	Low Isles	194.53–276.94 (230.44±21.86)	4.36–9.79 (7.13±1.53)
	GBR, Townsville–Whitsunday sector		
QMG303845	South Triangle Reef	159.95–228.63 (193.77±15.73)	2.07–3.77 (3.03±0.42)
	Vanuatu		
QMG306899	Malekula	152.04–426.54 µm (260.24±73.48)	1.54–3.29 µm (2.43±0.38)
P rara			
QMG319301	Holmes Reef, Coral Sea	171.82–309.65 (275.48±35.59)	2.93–6(4.8±0.72)
*P. hooperi**			
MHNG 18990 (holotype)	Kelso Reef, GBR	163–269 (232)	3–10 (6.4)
*P. terpenensis***			
QMG025039 (holotype)	Lizard Is., GBR	218–319 (237)	2.5–4.2 (3.4); 6.7–12.6 (8.7)
P. occidentalis			
NTM Z003366	Barrow Is., Western Australia	150.61–217.34 (183.8±19.74)	3.29–5.72 (4.48±0.73)

* From Van Soest et al. 1996 ** From Fromont (1993)

26m, 29.03.1993, S.D. Cook on FV ‘Clipper Bird’. CRRF 0CDN1807-X (fragment QMG304797): Coral sea, atoll 145km SW of Port Moresby, outer wall north side of atoll, 10°00.66’ S,145°39.90’ E, 20m, 22.10.1993, CRRF/NCI.

OTHER MATERIAL. (all QM material collected by Hooper, J.N.A. and party and, all CRRF material collected by CRRF under NCI contract, unless indicated otherwise): PAPUA NEW GUINEA: CRRF 0CDN8889-V: SE of Manus, 2°12.86’ S,147°13.68’ E, 40m, 24.06.2003. CRRF 0CDN1944-W: Rabaul, New Britain, 4°15.90’ S,152°20.45’ E, 40m, 7.11.1993. CRRF 0CDN1949-C: Madang Harbor, 5°12.50’ S,145°48.73’ E, 18m, 10.11.1993. CRRF 0CDN8208-H: Woodlark Is., 9°13.89’ S,152°25.56’ E, 24m, 10.01.2002. CRRF 0CDN8463-J: Goodenough Is., Cape Vogel, 9°35.61’ S,150°10.65’ E, 50m, 18.01.2002. CRRF 0CDN0561-S: Barakau, 9°38.64’ S,147°20.14’ E, 18m, 20.10.1992. CRRF 0CDN5812-A: Louisades; Calvados Is; 11°03.09’ S,152°28.62’ E, 10m, 1.06.1998. CRRF 0CDN8501-Y: SE Normanby Island, 10°06.33’ S,150°57.68’ E, 10m, 20.01.2002. QMG312928, Kupiano, 10°11.0501’ S,148°10.14’ E, 20m, 15.12.1996. CRRF 0CDN5981-L: Cape Rodney, 10°15.74’ S,148°23.07’ E, 18m, 12.06.1998. CRRF 0CDN5760-U: Milne Bay, 10°21.59‘ S,150°44.75‘ E, 23m, 27.05.1998. QMG312951, Keppel Point, Hood Bay, 10°8.1334‘ S,147°54.16‘ E, 35m, 16.12.1996. QMG312883, Motupore Is., 9°57.0167‘ S,147°28.16‘ E, 39m, 12.12.1996, ZMA Por. 08806, precise locality not specified, M.C. Díaz, 20–30m (cross ref. no. 90113). ZMA Por 17518, Milne Bay, 10°20.4 S,150°24.7 E, 12–21m depth, 27.05.2002, R.N. Sonnenschein. SOLOMON ISLANDS: QMG322938, Jackfish Pt, Mary I., Russell Is., 9°01.10’ S,158°43.77’E, 30m, 1.06.2006. VANUATU: QMG306899, Malekula Maskelyne, 16°30.05’ S, 167°49.01’ E, 50m, IRD/ORSTOM Noumea (ORSTOM R1656), 14.06.1996. AUSTRALIA, QUEENSLAND, GREAT BARRIER REEF, FAR NORTHERN SECTOR: QMG300293, Cockburn Is., 12°04.99’S, 143°18.99’E,11m, 11.12.1990. NTM Z004033, Cockburn Is., 12°05’ S,143°19.01’ E, 17m, 11.12.1990, NTM Z004042, Blanchard Reef, 13°23.3834’ S,143°44.39’ E, 14m, 12.12.1990. QMG320579, G320597: Wilson Reef, 13°40.3579’ S,144°13.6’ E, 36m, 1.07.2003. QMG320491, The Gut Rodder Reef, 13°54.787’ S,144°21.22’ E, 25m, 29.06.2003. CAIRNS–COOKTOWN SECTOR: QMG304310 Day Reef, 14°28.0667’ S, 145°31.04’ E, 25m, 7.04.1994. NTM Z004046, Howick Is., 14°29.55’ S,144°58.54’ E, 20m, 14.12.1990. QMG304178, Lizard Is., 14°39’ S,145°27’ E, 18m, 4.04.1994. NTM Z004062, Lizard Is., 14°40.0001’ S,145°27’ E, 15m, 17.12.1990. QMG304413, Lizard Is., 14°42’ S,145°27.14’ E, 15m, 11.04.1994. QMG305136, South Direction Is., 14°49.1501’ S,145°31.15’ E, 15m, 28.02.1995, QMG319070, Ribbon Reef No7, 15°08.164’ S,145°43.75’ E, 29m, 24.11.2001. QMG319054, Harrier Reef, 15°08.1971’ S,145°41.3’ E, 22m, 23.11.2001. QMG307657: Low Isles Sand Cay, 16°23.0501’ S,145°33.04’ E, 9m, 15.01.1997. QMG307714, Wooded Islet, Low Isles, 16°23.1334’ S,145°34.02’ E, 15m, 16.01.1997. QMG319560, NE of Cape Grafton, 16°43.911’ S,146°06.85’ E, 22m, 11.02.2002. QMG319151, Cape Tribulation, 16°06.5541’ S,145°38.63’ E, 16m, 25.11.2001. QMG321844, Fitzroy Is., 16°55.59’S, 145°59.29’ E, 20m, 24.11.2004. QMG321866, Normanby Is., 17°12.24’ S, 146°04.45’ E, 13m, 25.11.2004. QMG321893, Gibson Reef, 17°18.35’ S, 146°20.65’ E, 24m, 26.11.2004. QMG321952, Hall-Thompson Reef, 17°36.58’ S, 146°26.51’ E, 15m, 26.11.2004. QMG322002, Potter Reef, 17°44.59’ S, 146°29.32’ E, 22m, 27.11.2004. QMG322051, Farquharson Reef, 17°46.80’ S, 146°28.66’ E, 25m, 28.11.2004. TOWNSVILLE–WHITSUNDAY SECTOR: NTM Z002739, Myrmidon Reef, 18°10.0001’ S,147°23’ E, 15m, 1.01.1985, C.R.Wilkinson, QMG314345, Curacao Is., Palm Is., 18°40.825’ S,146°32.63’ E, 30m, 22.01.1999. QMG314448, Davies Reef, 18°49.555’ S,147°37.57’ E, 24m, 24.01.1999. QMG314550, Stanley Reef, 19°18.83’ S,148°02.56’ E, 30m, 25.01.1999. QMG314985, Hook-Hardy Reefs, 19°45.229’ S,149°10.76’ E, 26.7m, 5.06.1999. QMG303891, Hook Reef, 19°49.0167’ S,149°06.09’ E, 31m, 10.12.1993. QMG303845, Hook Reef, 19°49.0334’ S,149°07.02’ E, 21m, 8.12.1993. QMG315282, Round Reef, 19°57.6441’ S,149°37.28’ E, 20m, 6.06.1999. QMG314807: Hook Is., 20°03.93’ S, 149°55.41’ E, 15m, 3.06.1999. QMG314912, Cateran Bay, Border Is., 20°09.15’ S, 149°02.54’ E, 30m, 4.06.1999. QMG314939, Haslewood Is., 20°17.34’ S, 149°04.45’ E, 25.8m, 4.06.1999. QMG315320, Edgell Reef, 20°08.88’ S, 149°55.15’ E, 18 m, 6.06.1999. QMG315366, Stevens Reef, 20°32.57’ S, 150°06.43’ E, 30m, 7.06.1999. QMG315439, Chauvel Reef, 20°49.54’ S, 150°20.13’ E, 19m, 7.06.1999. MACKAY–CAPRICORN SECTOR: QMG315604, Coral Gardens, Heron Is., 23°27.0’ S, 151°53.99’ E, 10m, 5.06.1999, Garson M. and party. QMG321661, Heron Is., 23°26.48’ S, 151°53.68’ E, 30.2m, 10.11.2004. QMG307184, Heron Is., 23°27.08’ S, 151°54.12’ E, 25m, 6.08.1996. QMG307221, G307222, Sykes Reef, 23°25.13’ S, 152°03.03’ E, 25m, 7.08.1996. QMG307281, Snow’s Point, Heron Is., , 23°28.02’ S, 151°56.05’ E, 25m, 7.08.1996. QMG307498, Polmaise Reef, 23°33.05’ S, 151°39.15’ E, 12m, 12.08.1996. QMG307600, Heron Is., Wistari Reef Channel, 23°26.08’ S, 151°53.10’ E, 20m, 13.08.1996. QMG314073, Lady Musgrave Is., 23°53.32’ S, 152°25.6’ E, 21m, 22.02.1998. QMG305503, Price Cay, Swain Reefs, 21°47.08’ S, 152°27.02’ E, 30m, 25.07.1995. QMG305547: Price Cay, Swain Reefs, 21°47.08’ S, 152°27.07’ E, 30m, 26.07.1995. QMG305600, Frigate Cay, Swain Reefs, 21°44.08’ S, 152°25.03’ E, 32m, 27.07.1995. QMG317433, Surprise Reef, Swain Reefs, 21°59.15’ S, 152°20.71’ E, 30m, 5.02.2001. QMG317626, Reef 21-490, Swain Reefs, 21°36.31’ S, 152°22.19’ E, 17m, 8.02.2001. QMG317734, Star Reef, Swain Reefs, 21°30.0’ S, 152°26.14’ E, 30m, 11.02.2001. QMG317782, Reef 21-484, Swain Reefs, 21°34.61’

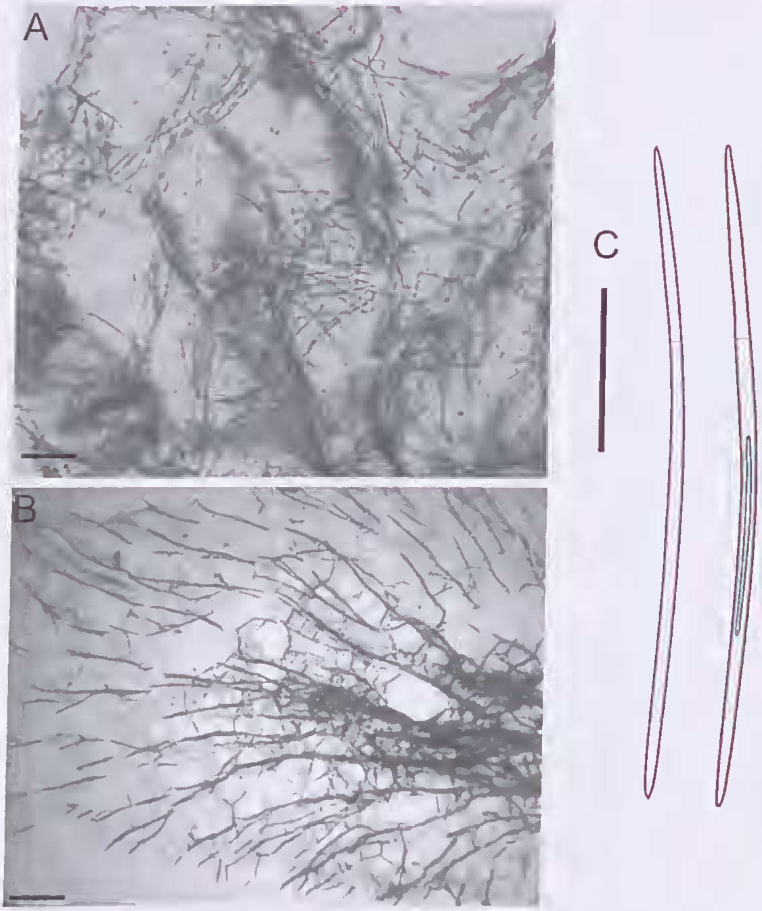

FIG. 2. *Pipestela candelabra* sp. nov. A, light micrograph of skeleton (Holotype, QMG320790, scale 100 µm). B, light micrograph of skeleton (0CDN 0561-S, scale 500 µm). C, diagram of oxeas (scale 50 µm).

S, 152°22.82’ E, 30m, 11.02.2001. QMG317822, Capricorn Reef, Swains Reef, 21°45.73’ S, 152°10.84’ E, 14m, 12.02.2001. QMG318035, northern Swain Reefs, 21°42.35’ S, 151°44.53’ E, 10.4m, 11 Mar, 2000. QMG314664, South Percy Is., 21°44.18’ S, 150°19.17’ E, 4.5m, 1.06.1999. QMG315481, Pompey Reefs, 21°29.74’ S, 151°09.80’ E, 26.2m, 8.06.1999. QMG318376, Pompey Reef, 21°12.75’ S, 151°11.72’ E, 21.8m, 18.03.2000. QMG318081, Rene’s Nook, T Line Reefs, 21°17.96’ S, 151°31.49’ E, 28m, 13.03.2000. QMG318224, Hard Line Reefs, 21°02/41’ S, 151°28.85’ E, 24m, 15.03.2000. QMG318250, Hard Line Reefs, 20°57.75’ S, 151°18.08’ E, 30m, 16.03.2000. QMG318313, Hard Line Reefs, 20°50.13’ S, 151°09.74’ E, 23.6m, 17.03.2000. QMG320004, G320029, Keppel Is., 23°09.55’ S, 151°04.23’ E, 17.6m, 4.11.2002. QMG320057: Keppel Is., 23°03.98’ S, 150°57.17’ E, 15.8m, 5.11.2002. QMG320114, Keppel Is., 23°07.08’ S, 150°59.45’ E, 17.4m, 6.11.2002.

CORAL SEA TERRITORIES: QMG306611, Wreck Reef, 22°10.78’ S, 155°11.47’ E, 30m, 15.01.1996.

DESCRIPTION. *Morphology.* Erect, 15–40cm tall on solid stalk of variable length and diameter. Growth form is arborescent, with cylindrical branches, lobes, hollow digits or tubes, 0.5–3cm in diameter, with walls of 3–5mm thick, with or without bulbous swellings along longitudinal length; sometimes fused together into a lamellar mass (Fig. 1A–D).

Colour. Orange, yellow or tan alive, yellow-beige in ethanol.

Oscula. Apical, single, large, conspicuous, on ends of tubes and on side or tips of branches, 3– 5mm diameter, sometimes covered with thin membrane

Texture. Flexible, moderately soft, velvety, rubbery, tough, not easily torn, can be sticky

Surface ornamentation. Optically smooth, fleshy. Slightly translucent, membranous with subdermal drainage channels

Ectosomal skeleton. Not specialised, membranous, pierced by choanosomal skeletal fibres.

Choanosomal skeleton. Slightly compressed near the axis of tubes; compressed at the stalk; with ascending and sinuous, plumose- pauci-multispicular ill-defined fibres, cored by oxeas (not occupying all of fibre diameter). Fibres either anastamosing or connected by single spicules or paucispicular short fibres at more or less regular intervals. Near-surface fibres become wispy. Interstitial free spicules abundant. Moderately heavy collagen present in mesohyl (Fig. 2A–B).

Spicules. Oxeas or strongyloxeas, thin (164–352 µm x 2–6 µm); some almost vestigial, curved, slightly bent, or sinuous, in a single size category

(Table 1); with axial channel occupying 10–90% of the total length frequently visible. Tips of oxeas are hastate, fusiform, or evenly rounded (Fig. 2C). Less frequent styles present in some specimens in the same size range. No microscleres

HABITAT. The species is generally found growing on slopes, walls, overhangs or caves of coral reefs in clear water (10–30m visibility), between 4.5–50m deep.

DISTRIBUTION. Papua New Guinea, Solomon Islands, Vanuatu, Coral Sea Territories and Great Barrier Reef, Australia (Fig. 3). This species is one of the most widely distributed sponges along the length and breadth of the GBR, from the coast to the outer barrier reefs, from near Torres Strait to the southern most reefs of the GBR. It is relatively common in some areas but mostly restricted to deeper waters (15–20m on reefs), and only rarely above about 10m depth.

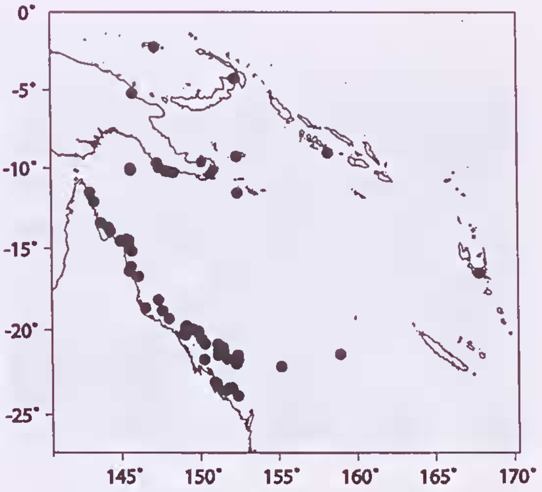

FIG. 3. Distribution of *Pipestela candelabra* based on all records from QM and NTM.

ETYMOLOGY. The species is named according to a colloquial name used by the Coral Reef Research Foundation (‘*Candelabra sponge*’) to identify the species during their collections for the U.S. National Cancer Institute. It is used as a noun in apposition.

REMARKS. The present species is nominated as the type species of the genus with a predominant growth form of tubes or cylindrical projections on a stalk. A similar growth form is found in species of the axinellid genus *Auletta*, but in that genus the choanosomal skeleton is reticulated and constructed by thick tracts of robust sinuous strongyles, styles and oxeas. Conversely, the skeleton of *P. candelabra* is a loose reticulation of wavy tracts of thin oxeas embedded in a spongin sheath or ill-defined fibres. In this respect the species might be related to *Cymbastela* which shares the possession of oxeas as the only type of spicule in the skeleton. *Cymbastela*, however, is typically cup-shape, also on a short stalk as in *Pipestela*, but never with cylindrical branches or ‘real’ tubes (not the tube-like projections, which are in fact cups within cups, commonly observed in some individuals of *Cymbastela*). The skeleton of *Cymbastela* spp is robust with a high spicular content giving the sponge a tougher and nearly incompressible consistency quite instead soft and low in spicule content as seen in *Pipestela*), The oxeas in species of *Cymbastela* are on average thicker (3.2–14.4 µm, Hooper and Bergquist, 1992) than the present species (2.4–7.1 µm; see Table 1). Some individuals (e.g. QMG312951, QMG307657) of *P. candelabra* however, have spicules of similar thickness when compared to *Cymbastela* spp. Changes in spicule thickness however, could be related to the availability of silica in the environment (Kelly-Borges & Vacelet, 1995) thus this character, although quite consistent through the examined specimens, cannot be considered a diagnostic indicator to separate species of these genera. Some specimens collected in Papua New Guinea (ZMA Por. 07892, ZMA Por. 10892) are also very similar to *P. candelabra* in growth form and external features and were found to have overlapping skeletal characters typical of *Axinella* (e.g. skeleton differentiated in axial and extra-axial regions and a presence of styles-subtylostyles with rounded ends) indicating that external shape of this species can be repeated at least in two other genera of Axinellidae (see Discussion below).

Records of this species under the name *Auletta constricta* (see synonymy) are based on the misinterpretation of Pulitzer-Finali's (1982) brief description and sparse illustrations. Re-examination of the holotype (MSNG 46930), collected from the Great Barrier Reef, shows that this record does not agree with *Pipestela candelabra*. The specimen described as *A. constricta* by Pulitzer-Finali (1982), despite some resemblance in the growth form, does not agree with the definition of *Auletta*, as the skeleton is not reticulated and robust strongyles are not present. The surface, which was described as covered with acute conules up to 1mm high is also not typical of either *Pipestela* or *Auletta*. Examination of the type slide

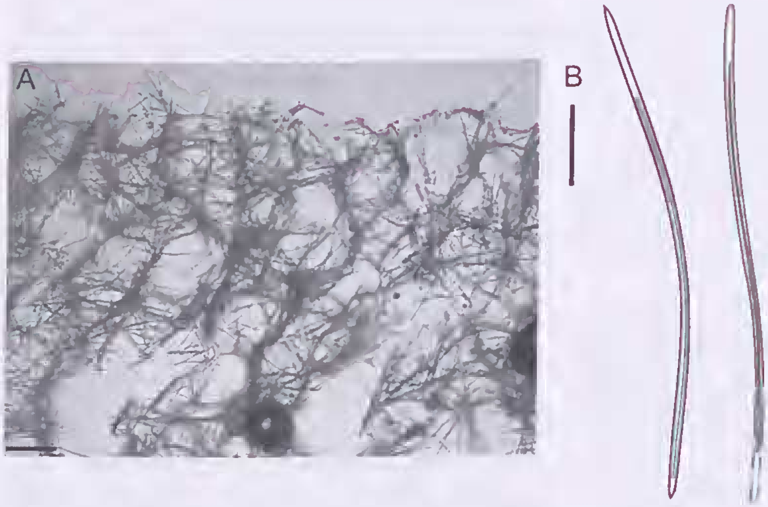

FIG. 4. *Pipestela rara* sp. nov. A, Holotype, QMG319301, light micrograph of skeleton (scale 200 µm). B, diagram of oxeas (scale 50 µm).

indicates the skeleton is mainly halichondroid, with distinct multispicular thick ascending and anastomosing tracts and abundant free spicules without any arrangement. Megascleres are slightly curved styles, in the size range reported in his publication, but the rare oxeas he mentions in his description were not found in the slide we examined. Based on the surface features, skeleton and spicule composition we here transfer it to the dictyonellid genus *Stylissa*.

Pipestela rara sp. nov
(Fig. 1E, 4)

MATERIAL EXAMINED. HOLOTYPE: QMG319301, Holmes Reef, Coral Sea Territories, Australia, 16°30.09' S,147°50.06' E, 19m, 9.02.2002, J.N.A Hooper et al.

DESCRIPTION. *Morphology.* Thickly encrusting spreading base covering dead coral, other sponges and invertebrates, with bulbous tubular fistules arising from base, predominantly fused, forming meandering ridges over the substrate. Fistules tapering at their ends forming chimneys up to 5cm high, 3cm diameter, with large apical oscule. Whole sponge up to 10cm thick in places including basal mat. The single known specimen consisted of a larger individual and a number of smaller clonal individuals in close proximity, together covering a large surface area of several square metres (Fig.1E).

Colour. Mauve-purple exterior, pinkish-beige interior alive; uniform drab brown when preserved.

Oscula. On terminal end of tubes, slightly constricted and with a thickened lip, darker in colour than the rest of the fistule or basal mat, diameter 3–6mm in life, 2–4mm when preserved.

Texture. Compressible, slightly fibrous, sticky, tearable when preserved.

Surface. Slightly honeycombed surface, smooth unornamented, with subsurface drainage canals visible in places on lateral sides of basal mat and larger fistules/ ridges, although ostia not easily seen.

Ectosomal skeleton. Membranous, with choanosomal spiculo-fibres penetrating the surface at right angles to form small brushes.

Choanosomal skeleton. More or less regular reticulation of ascending pauci- or multispicular tracts of spicules, without spongin fibres, connected by single spicules or short spicule tracts. Interstitial free spicules abundant. Mesohyl collagen light and homogenous. Some axial compression occurs further into the choanosome where the spicule tracts become less organised.

Spicules. Oxeas, flexuous, sinuous or slightly bent in one single size category, length 171.82–309.65 µm (275.48±35.59); width 2.93–6 µm (4.8±0.72). Tips of oxeas are pointy, hastate, telescoped, even or unevenly rounded, eroded or deformed; axial channel frequently visible.

HABITAT. Coral reef, 19m deep.

DISTRIBUTION. Known only from the type locality, a remote coral reef atop a 'seamount' in the Coral Sea.

ETYMOLOGY. *Rara,* Latin, feminine for *rarus* meaning scarce or hard to find and indicating the rarity of the species. It is intended to be adjectival in form.

REMARKS. The species differs from *Pipestela candelabra* in its growth form, colour and surface characteristics. Both species have a loosely reticulated skeleton and exclusively thin oxeas as megascleres. The skeletons of *P. candelabra* and *P. rara* are very similar but in *P. candelabra* spicule tracts are embedded in a spongin sheath forming ill-defined spongin fibres in most cases. Oxeas in *P. rara* are predominantly flexuous or sinuous with round tips. Spicule dimensions are comparable and axial channels are observed in the oxeas of both species.

Despite comprehensive surveys of sponge faunas on the GBR and Coral Sea over the past decade only a single specimen of this species has so far been encountered.

Pipestela hooperi
(Van Soest, Desqueyroux-Faúndez, Wright & König, 1996) comb. nov

Cymbastela hooperi Van Soest, Desqueyroux-Faúndez, Wright & König, 1996: 104.

MATERIAL EXAMINED. HOLOTYPE: MHNG 18990, Kelso Reef, Lucinda region, GBR, Queensland, Australia, 18°25'S,147°02'E, 6–9m depth, 1.03.1993, G.A.D. Wright.

REMARKS. This species was originally allocated to *Cymbastela* because it shares with other species of the genus a partially lamellate growth form, tough consistency, skeleton differentiated into axial and extra-axial regions and, type, size and telescoped endings of the oxeotes megascleres. Some differences however, make the species atypical of *Cymbastela*. Among these are the lamellate-flattened-encrusting habit, the unique feature of elevated oscula, and the relatively loose skeleton, formed by vaguely plumose paucispicular tracts of oxeas. The latter features agree with the definition of *Pipestela* and justify the new combination here proposed.

Pipestela hooperi and *P. rara* are both known only from single individuals found in coral reefs of the GBR and adjacent Coral Sea Territories, and are apparently rare in both areas. The morphology reported here for *P. rara and* in Van Soest, et al. (1996) for *P. hooperi* may not therefore be representative of the 'typical' growth forms of these species. Based on the available material the species are irregularly spreading on the substrate and lack any stalk; one growing into a modified cup- lamellate shape (*P. hooperi*) and the other into a mass of fused tubes forming ridges (*P. rara*), respectively. Oscula in both species are on elevations, rounded and short in *P. hooperi*, and on larger bulbous anastomosing fistules in *P. rara*. The two species differ also in colour, yellowish-brown in *P. hooperi* and mauve-purple in *P. rara*. The surface of *P. rara* has a honey-combed appearance not found in either *P. hooperi* or *P. candelabra*. Thus, in general, the external morphology of the two species differs substantially from *P. candelabra* but have in common the oscula placed on tubular elevations although these are not well developed in *P. hooperi*.

Pipestela candelabra, *P. rara* and *P. hooperi* are very similar in skeletal structure, all with paucispicular wavy tracts of exclusively thin oxeas (encased in lightly developed spongin fibres in *P.candelabra* and *P. hooperi*), forming a loose reticulation. Other characters shared by the three species are the presence of abundant free interstitial spicules, the shape and dimensions of the oxeas (Table 1), with an axial canal frequently observed.

Pipestela terpenensis
(Fromont, 1993) comb. nov.

Amphimedon terpenensis Fromont, 1993: 23; Garson, 1986: 35–36; Garson et al., 1993: 1011–1014; Garson et al., 1994: 509–516; Garson & Simpson, 2004: 164–170; Simpson & Garson, 2004: 939–948.

Cymbastela terpenensis; Van Soest et al. 1996: 107.

MATERIAL EXAMINED. HOLOTYPE: QMG25039, MacGillivray Reef, Lizard Island, Cooktown region, GBR, Queensland, Australia, 14°39' S, 145°27' E, 19m, 15.10.1987, J. Fromont.

OTHER MATERIAL. AUSTRALIA, QUEENSLAND, GREAT BARRIER REEF: QMG304435, Blue Lagoon, Lizard Is., Pinnacle, bommie on E.side, 14°42' S,145°27.14' E, 15m, 11.04.1994, J.N.A. Hooper et al. QMG304168, Turtle Beach, Lizard Is., headland N.side of bay, 14°39.0167' S,145°27' E, 15m, 4.04.1994, J.N.A. Hooper et al. QMG305393, Gannet Cay, S side reef, fore-reef slope, Swain Rfs, 21°59.0833 S,152°28.1'E, 24m, 23.07.1995, J.N.A. Hooper et al. NTM Z003170, Blue Lagoon, Lizard Is., Cairns region, 14°40.0001' S,145°28.01' E, 20m, 1.01.1987, A.W.D Larkum *et al.* NTM Z004037, W side of Nomad Reef, near Mason Is., Cockburn Is., Cape York region, 12°4.6001' S,143°18.8' E, 17m, 11.12.1990, J.N.A. Hooper. NTM Z004057, Blue Lagoon, Lizard Is., Cairns region, 14°40.0001' S,145°27' E, 15m, 17.12.1990, J.N.A. Hooper.

DISTRIBUTION. The species appears to be restricted to the GBR and overlaps with the distribution of other species of *Pipestela* (Fig. 5). It is found in coral reef habitats throughout the GBR, from Torres Strait to Masthead Island in the southern Bunker Group, and from coastal waters to the outer barrier reefs (QM database). It is more commonly found in lagoons and more sheltered waters where it has been found to grow to a reasonably large size (Fig. 1F), and its depth distribution is similar to that of *P. candelabra*.

REMARKS. This problematic species was originally thought to be related to the haplosclerid genus *Amphimedon* in the family Niphatidae. Although some features of the skeleton resemble members of that family, the absence of a proper tangential ectosomal skeleton is not in agreement with the diagnosis of *Amphimedon*. Based on this and other characteristics, such as the organisation of the choanosomal skeleton, the dimensions of the spicules, and chemical features (i.e. presence of isonitriles not previously recorded in other members of Haplosclerida, and an atypical chemical structure of fatty acids) Van Soest et al. (1996) transferred the species to the axinellid genus *Cymbastela*, with some hesitation as it differed from other species of that genus. Nevertheless, *A. terpenensis* was hypothesised to be related to *C. hooperi* (here also transferred to *Pipestela*), based on the common features of the loose structure of the choanosomal skeletons and the presence of isonitriles. This further supports the creation of a new genus to accommodate these species which were not typical of the homogeneous genus *Cymbastela*.

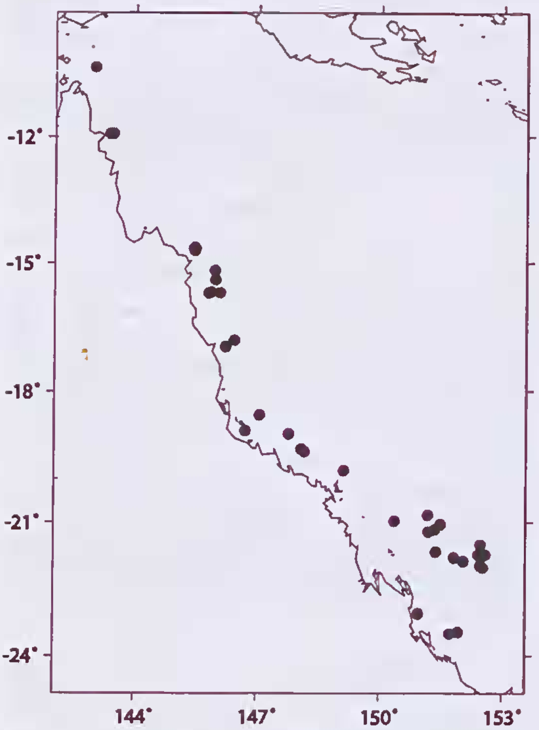

FIG. 5. Distribution of *P. terpenensis* based on all records from QM and NTM.

This species was described by Fromont (1993) as tall erect lamellate and/or coalescing branches with the appearance of flattened organ pipes, a feature that is vaguely reminiscent of *Pipestela candelabra* and *P. rara*. The colour is red-brown alive with cyanobacterial symbionts. Oscula are 2mm in diameter and located on the edges, raised ridges and nodes of the sponge. Skeleton is reticulated with paucispicular ascending tracts, encased in lightly developed spongin fibres and connected by short tracts and ending in narrow fans at surface. Spicules are exclusively oxeas, curved with fusiform or round tips and most with axial channel. All these features were confirmed in additional specimens examined here and agree with the definition of *Pipestela*.

Pipestela terpenensis produces large amounts of terpenes and its chemistry has been studied extensively (Garson et al., 1993; Garson et al., 1994; Garson & Simpson, 2004; Simpson & Garson, 2004).

Pipestela occidentalis sp. nov.
(Fig. 6)

MATERIAL EXAMINED. HOLOTYPE: WAM Z27509, 50m from shore, west side of Barrow Island, Cape Poivre, Western Australia, 20°48.1' S,115°19.5' E, 25m, 26.08.1988, D. Low Choy and NCI group (fragment NTM Z003366).

DESCRIPTION. *External morphology*. Erect, arborescent, stalked; 6.8cm length, 7.9cm width; branches solid, cylindrical, anastomosing laterally or dividing dichotomously, 4–5mm diameter, with tapering or short bifurcated tips, dividing regularly on thin stalk 6.5mm diameter; 16.8mm long.

Colour. Orange alive, beige in alcohol.

Oscula. Less than 5mm diameter, on small round elevations located in single rows along the sides and around the tips of the branches

Texture. Soft, flexible

Surface ornamentation. Smooth, microhispid perhaps velvety alive. Pierced with minute pores uniformly distributed; few branches marked with short and thin channels close to the branch tips

Ectosomal skeleton. Not specialised, pierced by choanosomal tracts.

Choanosomal skeleton. Plumose to plumo-reticulate; slightly differentiated in axial and extra-axial regions. Skeleton in axial region is halichondroid or vaguely reticulated; spongin fibres ill-defined. Extra-axial region with ascending plumose paucispicular to multispicular wavy tracts, anastomosing or connected by single spicules or short tracts, ending in brushes or fans of spicules near surface and piercing ectosome slightly.

Spicules. Oxeas, curved, fusiform; length 150.61–217.34 µm (183.8±19.74); width 3.29–5.72 µm (4.48±0.73). No microscleres.

Habitat. Coral reef

DISTRIBUTION. Western Australia. Known only from one specimen.

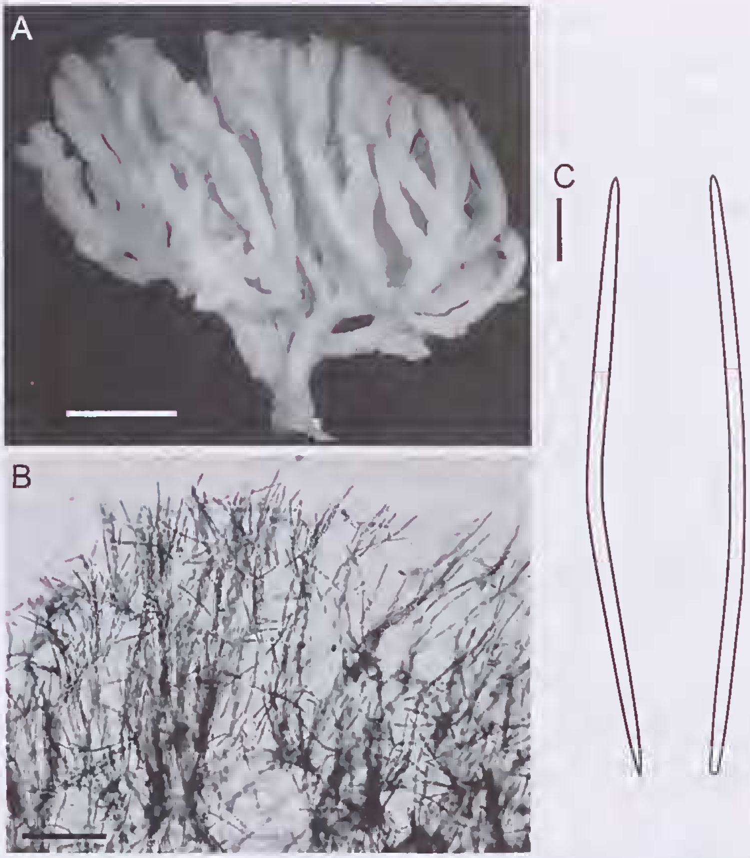

FIG. 6. *Pipestela occidentalis* sp. nov. A, Holotype, WAM Z27509, scale 2cm. B, light micrograph of skeleton (scale 200 µm). C, diagram of oxeas (scale 20 µm).

ETYMOLOGY. *Occidentalis*, Latin meaning from the west. It is intended to be adjectival in form.

REMARKS. The specimen agrees closely with *Pipestela candelabra* and it could indeed belong to this species but for its highly disjunct distribution in Western Australia, far outside the main population range of *P. candelabra*, so consequently we assign it to the genus as a new species. Disjunct distributions throughout northern Australia have been reported in numerous species of molluscs including gastropods and bivalves (e.g. Abbott, 1961; Houbrick 1978, 1992; Cernohorsky, 1991; Brunkhorst, 1993; Willan, 1993), and indeed also for several sponges, although not commonly so. The few documented examples include *Clathria (Thalysias) coppingeri*, which is mainly northwestern Australian in distribution but with rare incursions into SE Queensland (Hooper, 1996), and *Raspailia (Raspaxilla) compressa*, which was discovered on the mid-east and mid-west coasts of Australia, but not in between despite intensive benthic surveys (Hooper, 1991; Hooper & Ekins, 2004). Conversely, there are many instances of east-west coast 'sibling species pairs' that are morphologically similar but distinct species, including sponges (e.g. *Cymbastela stipitata* from NW Australia and *C. concentrica* from NE Australia, with Torres Strait being the major species turnover point (Hooper & Ekins, 2004). Consequently, we consider that a circum-tropical Australian distribution of a single morphospecies '*P. candelabra*' is inconclusive. Molecular data or other types of evidence is required to test conspecificity or otherwise between this east–west coast species pair, and also their relationships with populations of *P. candelabra* in Papua New Guinea, Solomon Islands, Vanuatu and the Coral Sea Territories.

DISCUSSION

As for other genera of Axinellidae the new genus *Pipestela* is defined by a set of morphological and skeletal characters that is not unique (i.e. these characters appear in some other genera of the family, especially *Cymbastela*, but occur in a unique combination). Species previously assigned to *Cymbastela* (i.e. *C. hooperi* and *C. terpenensis*) are transferred here to *Pipestela* based on shared characteristics with *P. candelabra*, *P. occidentalis* and *P. rara* (i.e. skeleton with a loose reticulation of plumose paucispicular tracts of relatively thin oxeas). We propose that *Cymbastela* be restricted to cup-shaped species bearing mainly robust oxeas and with a typical axinellid plumoreticulate skeleton of well-defined multispicular plumose tracts, coring well to poorly developed spongin fibres, compared with laminar, branching or tubular growth forms with a loose reticulation of mostly paucispicular tracts encased sometimes in poorly developed spongin fibres, in *Pipestela*.

Stalked and branching, thin, tubular forms similar to *Pipestela* are also found in species of *Auletta*, such as *A. sycinularia* with a type of spiculation similar to *Phakellia* and *Acanthella* (i.e. robust styles, sinuous strongyles). Other species with this type of growth form are *Auletta aurantiaca* Dendy, 1887: 92, *A. lyrata* sensu Dendy, 1905: 194, *A. lyrata glomerata* Dendy, 1905: 195, *A. lyrata crassispiculata* Dendy, 1905: 195, *A. lyrata brevispiculata* Dendy, 1905: 195 and *A. elongata* Dendy, 1905: 195. In this group of species the spicule composition consists mainly of oxeas and styles as in species of *Axinella* and the sinuous strongyles are lacking. Therefore growth form cannot be used as a diagnostic feature of these genera, especially *Pipestela* and *Auletta*.

Pipestela could potentially be confused with some haplosclerids, such as *Amphimedon*, to which *P. terpenensis* was originally allocated, but the absence of an ectosomal skeleton indicates an affinity with Halichondrida rather than Haplosclerida. The removal of this species from its original genus leaves Indo-Pacific species recognised as *Amphimedon*, as a more cohesive group characterised by blue spectrum colouration and a sticky exudates. Conversely, a so far undescribed specimen collected in Oman (ZMA Por. 13896) has many of the diagnostic features of *Pipestela*, including the tubular branching growth form, choanosomal skeleton and spicule composition and dimensions, but also has a tangential ectosomal skeleton characteristic of *Amphimedon*, indicating that might better be allocated to that genus. Assuming that the diagnostic morphological characters proposed for *Pipestela* are plesiomorphic, its affinities with members of Axinellidae become uncertain and phylogenetic studies using appropriate genetic markers (Alvarez, in progress) are required to confirm the position of the new genus in the sponge classification.

A variety of novel chemical compounds have been discovered from *Pipestela* species. *Pipestela candelabra* produces at least three types of milnamide (A-C), a novel compound with toxic cytoskeletal activity (e.g. microtubule depolymerization, microfilament disruption) (Sonnenschein et al., 2004). *Pipestela terpenensis* and *P. hooperi* produce sesqui- or diterpenes derived from isonitriles of similar chemical structure (e.g. di-iso-cyano-adociane). Other isonitrile derivates have been isolated from halichondrid sponges but not from haplosclerids (Van Soest et al., 1996b and references within), supporting the allocation of this new genus to the Axinellidae in Halichondrida.

Extensive collection records of *Pipestela* species indicate that the genus is distributed mainly throughout northeastern Australasia, extending from the southern GBR to northeastern PNG, the Australian Coral Sea Territories, the Solomon Is and also one record in central Vanuatu, and its species are always associated with coral reefs in relatively clear water. The absence of *Pipestela* in the characteristically more turbid waters of Arafura and Timor Seas, and its reappearance in northwestern Australia (albeit indicated so far by only a single specimen found off the coast of Western Australia which closely resembles *P. candelabra*), supports the hypothesis that these sponges are not generalists but niche specialists, surviving only in clear water coral reef habitats (e.g. Hooper, 1994), and thus potentially having a much broader distribution across the Indo-west Pacific than is presently known. Molecular studies are needed to determine the precise affinities of the material collected from Western Australia, and further effort is required to search for additional outlying populations either side of the known range to precisely define the distribution limits of both *P. candelabra* and the general distribution of the genus.

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